Evaluation of salt-tolerant forages for sequential water reuse systems
II. Plant–ion relations

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Abstract

Implementation of the saline drainage water reuse system proposed for the westside of the San Joaquin Valley (SJV) of California requires development of sustainable cropping systems, which incorporate useful, salt-tolerant agronomic species. Ion composition in the saline drainage effluents present in the SJV is unique, with Na^+, SO_4^{2-}, Cl^-, Mg^{2+} and Ca^{2+} predominating in that order. To identify potentially suitable crops for reuse systems, 10 forages were tested in greenhouse sand cultures located at USDA-ARS George E. Brown Jr. Salinity Laboratory, Riverside, California. Crops were: alfalfa (*Medicago sativa* L.) cvs. 'Salado' and 'SW 9720'; narrowleaf trefoil (*Lotus glaber* Greene) cv. 'PI 608022'; broadleaf trefoil (*L. ulginosus* Schk.) cv. 'Big'; tall wheatgrass (*Agropyron elongatum* (Host) Beauv.) cv. 'Jose'; alkali sacaton (*Sporobolus airoides* Torr.); kikuyugrass (*Pennisetum clandestinum* Hochst. Ex Chiov.) cv. 'Whittet'; paspalum (*Paspalum vaginatum* Swartz) cvs. PI '299042' and 'Polo'; and bermudagrass (*Cynodon dactylon* L. Pers.) cv. 'Tifton'. Two saline treatments, 15 and 25 dS m^{-1}, were imposed. Shoots were sub-sampled for mineral ion analysis when the forages were harvested. Patterns of shoot ion concentrations were unique for each species and varied with salinity level, external ion ratios, harvest date and plant age. Plant preference for K^+ over Na^+ did not appear to be a reliable predictor of salt tolerance. Salt-tolerant crops, such as kikuyugrass and bermudagrass, were highly selective for K^+ ($S_{K,Na} \sim 200$ to 400), whereas selectivity

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coefficients for the equally salt-tolerant grasses, alkali sacaton and tall wheatgrass, ranged from 20 to 40. The forages were highly selective for K^+ over Mg^{2+} despite unusually low K^+:Mg^{2+} ratios in the external solutions. Total-S in the herbage was high and generally increased as external SO_4^{2-} increased. Based on sustained nutritional health and lack of visual signs of toxicity or deficiency symptoms, several of the forages tested show promise as suitable candidates for the saline–sodic water reuse systems.

1. Introduction

Limited access to natural drainage in the westside of the San Joaquin Valley (SJV) of California has led to strategies for on-farm or regional reuse of saline drainage waters for irrigation of selected crops (Grattan and Oster, 2003). However, the suitability of these drainage waters for crop production will depend on the potential hazards they pose to sustained crop growth. Relevant criteria for evaluating water quality include not only total salt concentration, but also the individual concentrations of specific ions contributing to salinity (Rhoades et al., 1992). Salt-tolerant forages may play an important role in drainage water reuse management provided the unique ion composition of the saline drainage effluents does not adversely affect the balance of essential plant mineral nutrients and limit the sustainability of the cropping system (Oster et al., 1999). Solutions prepared to simulate these drainage waters have been used at this laboratory to test the salt tolerance of a wide range of horticultural, agronomic, and alternative crops. Common trends in ion concentrations in above-ground organs were observed in our previous studies, which emphasize the interactive effects of substrate composition on ion availability, uptake, transport, partitioning within the plant, and ultimately, on plant health and productivity (Shannon et al., 2000; Ferguson et al., 2002; Rogers et al., 1998; Dierig et al., 2003).

The objective of this facet of the greenhouse study was to investigate ion relations of 10 forage crops irrigated with waters prepared to simulated SJV saline drainage effluents.

2. Materials and methods

Ten forages were chosen for this study: alfalfa cvs. 'Salado' and 'SW 9720'; narrow leaf trefoil; broadleaf trefoil cv. 'Big'; tall wheatgrass cv. 'Jose'; alkali sacaton; kikuyugrass cv. 'Whittet'; paspalum cvs. PI 299042 and 'Polo', and bermudagrass cv. 'Tifton'. The experiment was conducted from 17 July 2000 to 1 August 2001 in greenhouse sand tank cultures at the USDA-ARS, George E. Brown Jr. Salinity Laboratory, Riverside, CA. Growth conditions, additional experimental details and source of the plant materials are given in the companion paper (Grattan et al., 2004a). Irrigation waters were analyzed by inductively coupled plasma optical emission spectrometry (ICPOES) to confirm that target ion concentrations were maintained. Chloride in the solutions was determined by coulometric–amperometric titration. Supplemental potassium, nitrate and phosphate, were

added on January 2001 and again on 5 April 2001 to bring concentrations in the irrigation waters to target concentrations.

At each harvest, herbage was cut about 8–10 cm above the surface of the sand. Shoot material was weighed, washed in deionized water, dried in a forced-air oven at 70 °C for 72 h, re-weighed, and ground to pass a 60-mesh screen. Total-S, total-P, Ca^{2+}, Mg^{2+}, Na^+, and K^+ were determined on nitric–perchloric acid digests of the tissues by ICPOES. Chloride was determined on nitric–acetic acid extracts by coulometric–amperometric titration.

Ion selectivity coefficients were determined on plant samples harvested prior to the first replenishment of substrate K^+ salts. Coefficients were calculated from the ratio of specific ions in the plant divided by the ratio of those ions in the external medium (Flowers and Yeo, 1988). Statistical analyses were performed by analysis of variance with mean comparisons at the 95% level based on Tukey's studentized range test. SAS release version 8.02 was used (SAS Institute Inc., 2001).

3. Results and discussion

3.1. Mineral ion concentrations

Concentrations of Ca^{2+}, Mg^{2+}, Na^+, K^+, Cl^-, and total-S, determined at each forage harvest, are expressed as a function of time under salinity (Figs. 1–10). Shoot ion concentration patterns were unique for each species and varied with salinity treatment, plant age, and frequently, among harvest dates. With the exception of broadleaf trefoil, all species remained healthy during the experimental period and no visible symptoms of ion
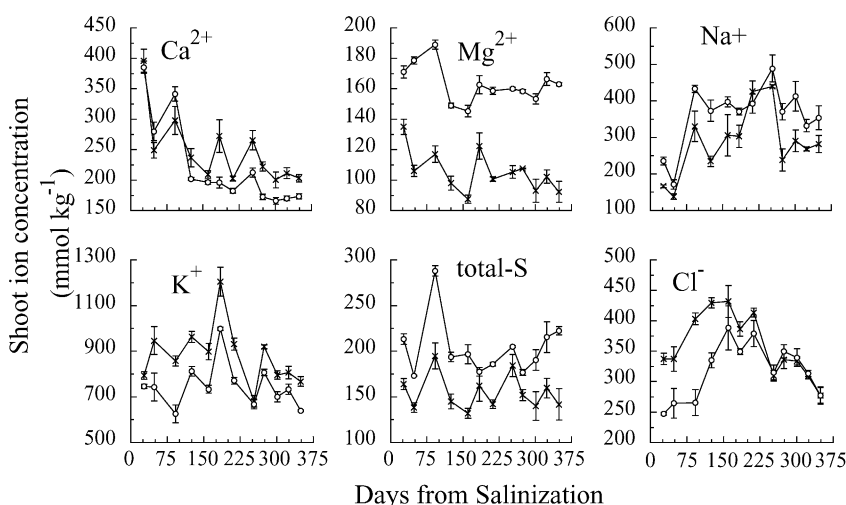

Fig. 1. Shoot Ca^{2+}, Mg^{2+}, Na^+, K^+, total-S, and Cl^- determined in sequential harvests of alfalfa cv. 'Salado' grown at two salinity levels [EC = 15 (×) or 25 dS m^{-1} (○)]. Salinity applied, 14 Aug 2000; first harvest, 11 Sep 2000. At each harvest, values are the means of three replications; error bars = S.E.

Fig. 2. Shoot Ca^{2+}, Mg^{2+}, Na^+, K^+, total-S, and Cl^- determined in sequential harvests of alfalfa cv. 'SW 9720' grown at two salinity levels [EC = 15 (×) or 25 dS m^{-1} (○)]. Salinity applied, 14 Aug 2000; first harvest, 11 Sep 2000. At each harvest, values are the means of three replications; error bars = S.E.
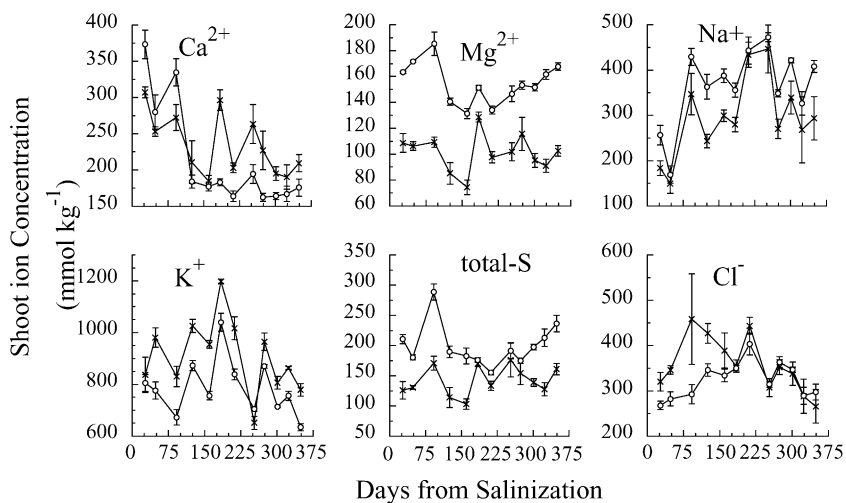
toxicities or nutrient deficiencies were observed. Broadleaf trefoil plants became weak and chlorotic in the 15 dS m^{-1} treatment and began to die shortly after imposition of higher salinity; therefore, ion concentrations from the 25 dS m^{-1} treatment are available for only a single harvest.
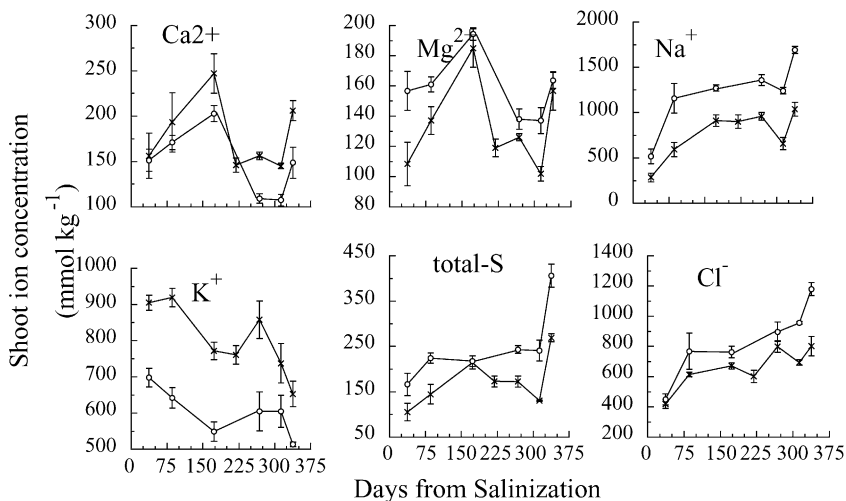

Fig. 3. Shoot Ca^{2+}, Mg^{2+}, Na^+, K^+, total-S, and Cl^- determined in sequential harvests of narrowleaf trefoil grown at two salinity levels [EC = 15 (×) or 25 dS m^{-1} (○)]. Salinity applied, 25 Aug 2000; first harvest, 2 Oct 2000. At each harvest, values are the means of three replications; error bars = S.E.

Fig. 4. Shoot Ca^{2+}, Mg^{2+}, Na^+, K^+, Total-S, and Cl^- determined in sequential harvests of broadleaf trefoil grown at EC = 15 dS m^{-1} ($\times$) and a single harvest of plants grown at 25 dS m^{-1} ($\bigcirc$)]. Salinity applied, 25 Aug 2000; first harvest, 2 Oct 2000. At each harvest, values are the means of three replications; error bars = S.E.

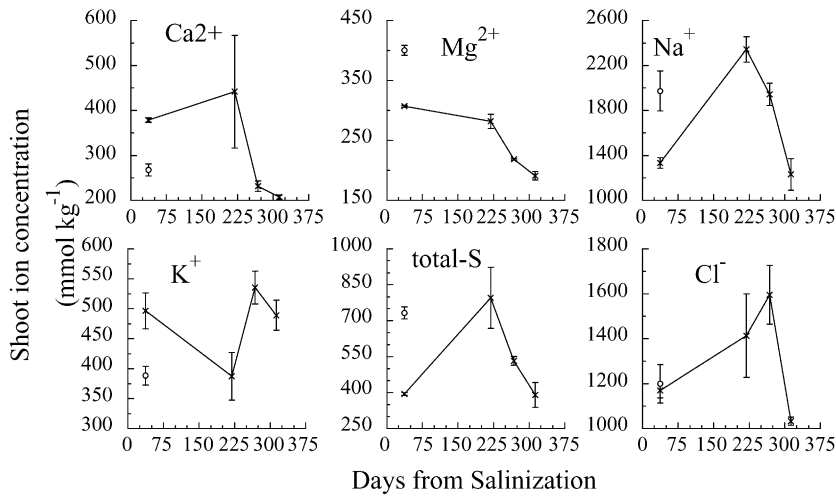### 3.1.1. Calcium

Temperate leguminous forages generally contain three- to four-fold higher levels of Ca^{2+} than temperate grasses (Underwood and Suttle, 1999). This relationship was also observed in the present experiment, particularly during the early harvests, when Ca^{2+} was two to five times higher in alfalfa than in any of the grass species. Over-the-season, shoot-
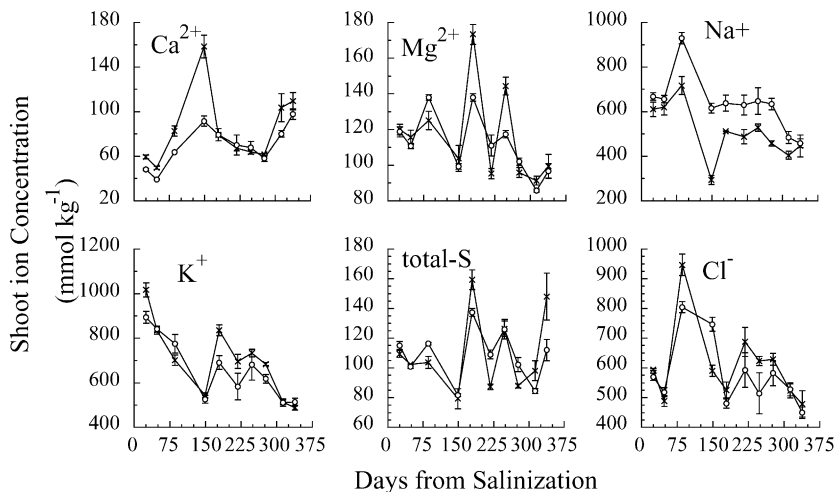

Fig. 5. Shoot Ca^{2+}, Mg^{2+}, Na^+, K^+, total-S, and Cl^- determined in sequential harvests of tall wheatgrass cv. 'Jose' grown at two salinity levels [EC = 15 ($\times$) or 25 dS m^{-1} ($\bigcirc$)]. Salinity applied, 25 Aug 2000; first harvest 20 Sep 2000. At each harvest, values are the means of three replications; error bars = S.E.

Fig. 6. Shoot Ca^{2+}, Mg^{2+}, Na^+, K^+, total-S, and Cl^- determined in sequential harvests of alkali sacaton grown at two salinity levels [EC = 15 (×) or 25 dS m^{-1} (○)]. Salinity applied, 25 Aug 2000; first harvest 20 Sep 2000. At each harvest, values are the means of three replications; error bars = S.E.

Ca in alfalfa irrigated with moderately saline water was high (range = 211–396 mmol kg^{-1}, mean = 247 mmol kg^{-1}) compared with kikuyugrass (range = 66–162 mmol kg^{-1}, mean = 101 mmol kg^{-1}) or tall wheatgrass (50–158 mmol kg^{-1}, mean = 84 mmol kg^{-1}). Calcium in alfalfa decreased over time, whereas, by the end of the experiment, Ca^{2+} content in all of the grasses was significantly higher than in the early harvests.

Fig. 7. Shoot Ca^{2+}, Mg^{2+}, Na^+, K^+, total-S, and Cl^- determined in sequential harvests of kikuyugrass cv. 'Whittet' grown at two salinity levels [EC = 15 (×) or 25 dS m^{-1} (○)]. Salinity applied, 22 Aug 2000; first harvest 19 Sep 2000. At each harvest, values are the means of three replications; error bars = S.E.
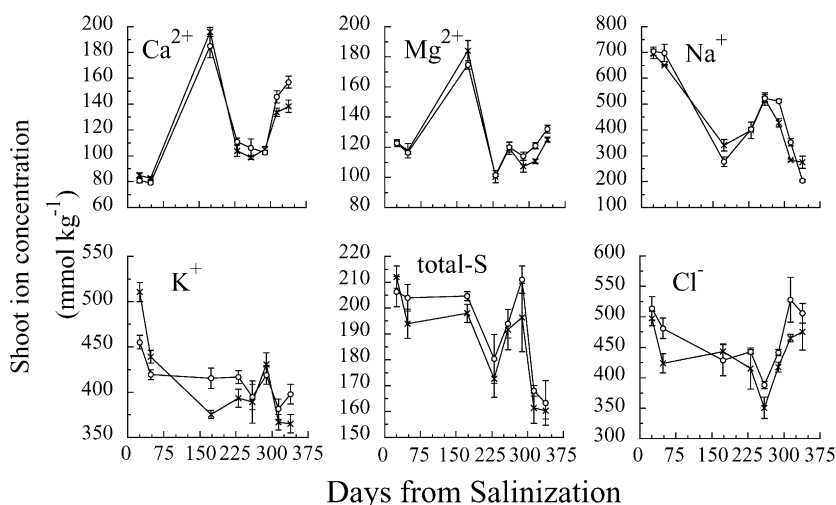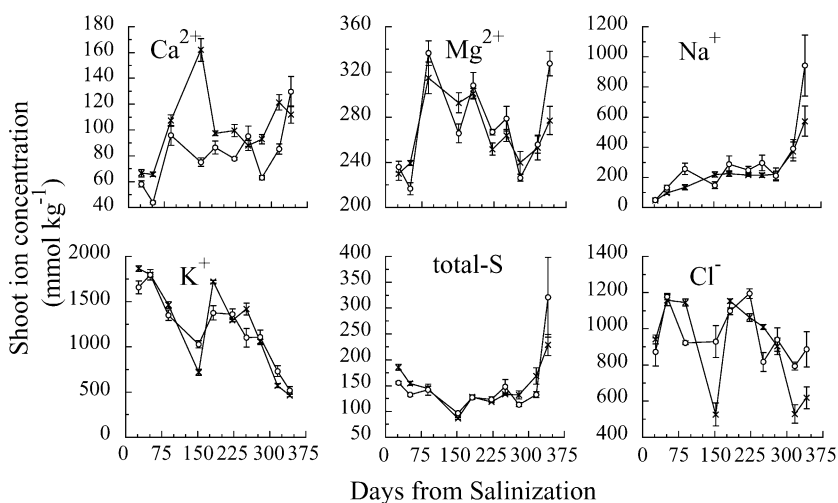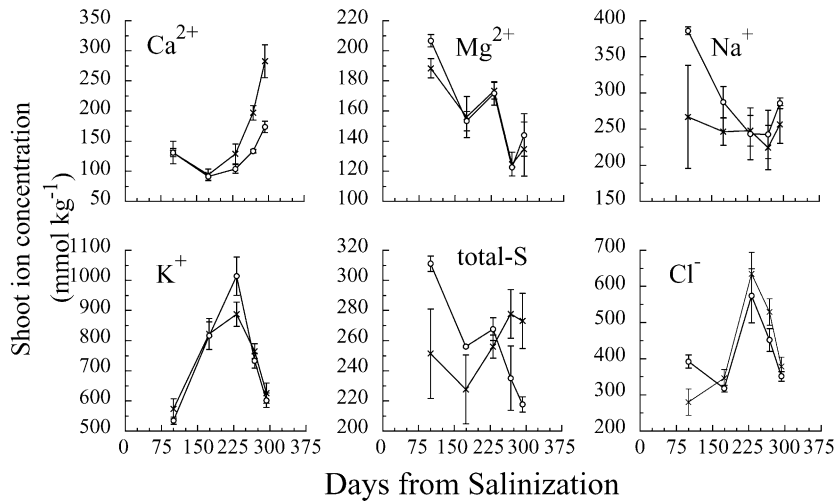
Fig. 8. Shoot Ca^{2+}, Mg^{2+}, Na^+, K^+, total-S, and Cl^- determined in sequential harvests of paspalum PI 299042 grown at two salinity levels [EC = 15 ($\times$) or 25 dS m^{-1} ($\bigcirc$)]. Salinity applied, 9 Oct 2000; first harvest, 18 Jan 2001. At each harvest, values are the means of three replications; error bars = S.E.

Herbage Ca^{2+} tended to decrease as salinity increased from 15 to 25 dS m^{-1}, even though external Ca^{2+} increased slightly. Under saline conditions, decreases in Ca^{2+} uptake are due to reactions in the soil solution (e.g., ion interactions and increases in ionic strength) that reduce Ca^{2+} availability to the plant (Suarez and Grieve, 1988; Grattan and Grieve, 1999).

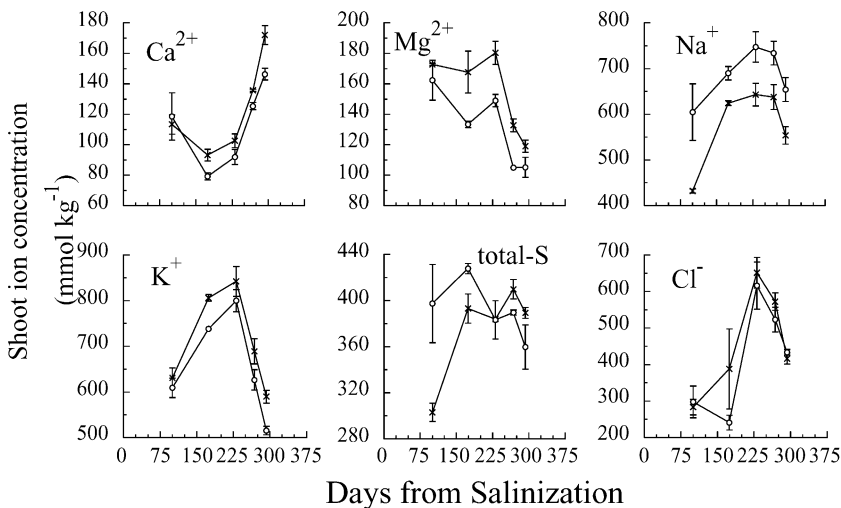Fig. 9. Shoot Ca^{2+}, Mg^{2+}, Na^+, K^+, total-S, and Cl^- determined in sequential harvests of paspalum cv. 'Polo' grown at two salinity levels [EC = 15 ($\times$) or 25 dS m^{-1} ($\bigcirc$)]. Salinity applied, 9 Oct 2000; first harvest, 18 Jan 2001. At each harvest, values are the means of three replications; error bars = S.E.
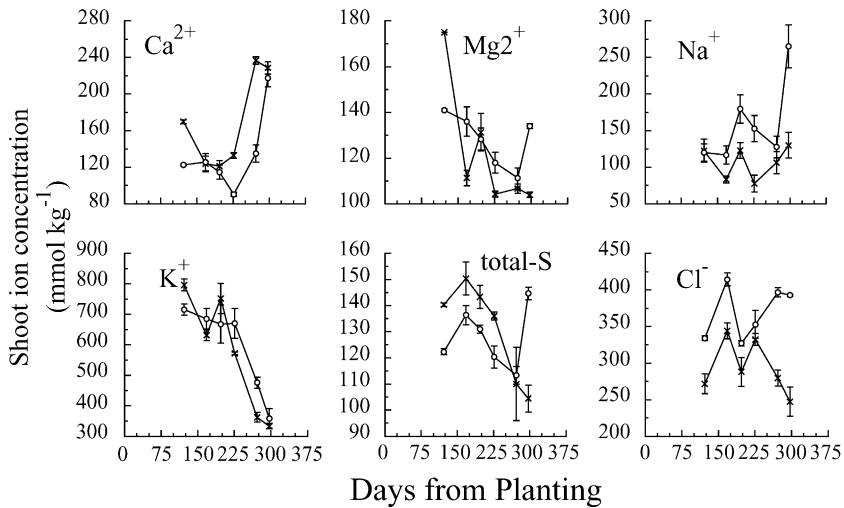
Fig. 10. Shoot Ca^{2+}, Mg^{2+}, Na^+, K^+, total-S, and Cl^- determined in sequential harvests of bermudagrass grown at two salinity levels [EC = 15 ($\times$) or 25 dS m^{-1} ($\bigcirc$)]. Stolons planted in pre-salinized sand tanks, 5 Oct 2000; first harvest, 15 Feb 2001. At each harvest, values are the means of three replications; error bars = S.E.

3.1.2. Magnesium

The two-fold increase in external Mg^{2+} in concert with increased salinity resulted in significantly higher shoot-Mg in the legumes at all harvests. Response to higher substrate Mg^{2+} by many of the grasses, however, was variable among harvests. Often there were no differences between salinity treatments and in some cases, shoot-Mg was significantly higher at low, rather than at high external Mg^{2+}, e.g., tall wheatgrass harvests 5 and 7 (Fig. 5) and kikuyugrass, harvest 4 (Fig. 7). The response of 'Polo' paspalum (Fig. 9) was unique in that herbage Mg was higher at every harvest, when the plants were irrigated with waters containing 14 mol m^{-3} Mg^{2+} than with more saline waters with twice as much Mg^{2+}. Magnesium was strongly accumulated by kikuyugrass (Fig. 7) with concentrations ranging from 220 to 340 mmol kg^{-1} (mean = 266 mmol kg^{-1}). Shoots of broadleaf trefoil from the single harvest of plants irrigated with 25 dS m^{-1} waters were also high in Mg^{2+}.

3.1.3. Sodium

The nearly two-fold increase in external Na^+ concentration resulted in a significantly higher increase in herbage-Na at all harvests of narrowleaf trefoil (Fig. 3) and 'Polo' paspalum (Fig. 9). This response was generally true for alfalfa (Figs. 1 and 2), tall wheatgrass (Fig. 5) and bermudagrass (Fig. 10), but numerical differences in some harvest samples were not significant.

Natrophobic species, sometimes called "Na excluders", have evolved mechanisms for restricting Na^+ accumulation in shoot tissues (Marschner, 1995). Sodium exclusion by the well-known natrophobes, alfalfa (Figs. 1 and 2), and kikuyugrass (Fig. 7) (Underwood and Suttle, 1999) was more effective during the early stages of plant growth. Sodium uptake in

bermudagrass was excluded to a greater extent than in any of the other forages (Fig. 10). Shoot-Na was high in the trefoils (Figs. 3 and 4), which are classified as Na-accumulators, or ''natrophiles'' (Underwood and Suttle, 1999).

The salt sensitivity of broadleaf trefoil may be at least partially due to excessive accumulation of Na^+ (Fig. 4). Death of broadleaf trefoil plants, which commenced shortly after the first harvest, suggests that loss of root membrane integrity permitted passive permeability of Na^+ to plant tissue where it reached toxic levels.

3.1.4. Potassium

Potassium concentrations in the forages were generally depressed as salinity increased from 15 to 25 dS m^{-1}. For legumes, the effect was highly significant at most harvests (Figs. 1–3). Potassium in the irrigation waters was replenished twice during the experiment. Once K^+ concentration returned to target levels, shoot-K of some species increased at both salinity levels (e.g., alfalfa, harvest 6; tall wheatgrass, harvest 5). Shoot-K in narrowleaf trefoil (harvest 3) and alkali sacaton (harvest 3) appeared to be affected by the second addition of supplemental K^+, but not by the first. Kikuyugrass was a strong K^+ accumulator in the two early harvests, and showed a significant positive response to the first addition of K^+ salts at harvest 5. Shoot-K in paspalum cultivars and bermudagrass tended to decrease even after addition of supplemental K^+ on day 237 (Figs. 8 and 9).

3.1.5. Sulfur

Forage crops differ markedly in S requirements for optimum growth, as shown by their tissue S-content, i.e., grasses 31–47 mmol kg^{-1}; legumes 78–93 mmol kg^{-1} (Underwood and Suttle, 1999). Sulfate concentrations in SJV waters are typically high (Deverel et al., 1984) and S accumulation by vegetables and woody perennials irrigated with water prepared to simulate drainage effluents generally greatly exceed their nutritional requirements (Shannon et al., 2000; Ferguson et al., 2002). Over the duration of the experiment, shoot-S concentrations in 'Salado' alfalfa grown at 25 dS m^{-1} ranged from 173 to 288 mmol kg^{-1} (mean = 203), whereas total-S in tall wheatgrass ranged from 82 to 137 mmol kg^{-1} (mean = 109). Total-S was higher in the paspalums than in the other grasses. It is not known whether paspalum is an example of an unusually strong S accumulator, or if the S requirement for the species is higher than for other grasses. Total-S in broadleaf trefoil shoots from the single harvest of the 25 dS m^{-1} treatment was more than twice as high as in the other legumes.

In response to the nearly two-fold increase in substrate-SO_4, total-S increased significantly in alfalfa (Figs. 1 and 2) and trefoil (Fig. 3) at most harvest dates, although the effect was more variable in the grasses. Differences in total-S accumulation due to increases in external SO_4^{2-} were rarely significantly different for tall wheatgrass (Fig. 5), alkali sacaton (Fig. 6), and kikuyugrass (Fig. 7). Total-S in the two early harvests of both paspalum cultivars was significantly higher in the 25 dS m^{-1} treatment than at the lower salinity, but this effect reversed as the plants aged (Figs. 8 and 9). Bermudagrass showed the opposite response where total-S was higher at lower external SO_4^{2-} in herbage samples collected at the first four harvests, but at the last harvest, it was significantly lower than in plants grown at 25 dS m^{-1} (Fig. 10).

3.1.6. Chloride

Shoot-Cl in alfalfa sampled over the first four harvest dates was significantly higher in plants irrigated with moderately saline waters than at higher external Cl^- (Figs. 1 and 2). At subsequent alfalfa harvests, numerical differences in shoot-Cl were not significant. Shoot-Cl in both paspalum cultivars (Figs. 8 and 9) also tended to be higher in the 15 dS m^{-1} treatment than at 25 dS m^{-1}, an effect that was also observed in some harvests of tall wheatgrass (Fig. 5), alkali sacaton (Fig. 6), and kikuyugrass (Fig. 7). Shoot-Cl in narrowleaf trefoil (Fig. 3) and bermudagrass (Fig. 10) was consistently higher at all harvests as salinity increased.

3.2. Ion ratios and interactions

Plant performance may be adversely affected by salinity-induced nutrient imbalances that result from effects of salinity on nutrient availability, competitive uptake, transport and partitioning within the plant (Grattan and Grieve, 1999). The majority of these interactions are directly related to the concentrations and ratios of ions in the rootzone. Ion compositions typically present in saline agricultural effluents in the SJV often result in unusual ratios of Na^+/Ca^{2+}, Na^+/K^+, Mg^{2+}/K^+, Mg^{2+}/Ca^{2+}, Cl^-/NO_3^-, and SO_4^{2-}/Cl^-. The influence of these external ion ratios on ion accumulation by salt-stressed plants is complex. Salinity dominated by Na^+ salts, for example, often reduces Ca^{2+} activity in the external media and limits its availability to the plant (Suarez and Grieve, 1988). Magnesium is also strongly competitive with Ca^{2+} and may displace Ca^{2+} from extracellular binding sites within plant organs to further disrupt metabolic availability of Ca^{2+}. Plant growth may be reduced, when the external Mg^{2+}/Ca^{2+} increases above 1 (Carter et al., 1979).

Sodium-induced K^+ deficiencies have been implicated in growth and yield reductions of salt-stressed crops. Maintenance of adequate levels of K^+ is essential for plant survival under saline conditions due principally to its contribution towards lowering the osmotic potential in root cells, a pre-requisite for controlling solute transport and water balance. Interactive effects due to increase in substrate Na^+, however, may reduce crop growth by disrupting root membrane integrity and altering selectivity of the root system for K^+ over Na^+ (Tester and Davenport, 2003).

Many researchers have suggested that the K^+/Na^+ ratio in tissues of glycophytes should be >1 to supply the K^+ necessary for the normal functioning of metabolic processes (Ashraf, 1994; Maathuis and Amtmann, 1999). According to this criterion, the K^+/Na^+ ratios measured at both salinity levels for kikuyugrass, paspalum, bermudagrass, and possibly, alfalfa would be considered adequate for normal plant growth (Table 1). The ratios for tall wheatgrass and alkali sacaton at both salinity levels, however, were lower than recommended. For all species, the ratio fell as salinity and substrate Na^+ increased. The warm season grasses, kikuyugrass and bermudagrass, showed the strongest preference for K^+ over Na^+. Coefficients for alfalfa, the trefoils and kikuyugrass decreased as salinity increased, whereas values for tall wheatgrass, alkali sacaton, the paspalums, and bermudagrass increased. Selectivity coefficients averaged over the season for alfalfa, narrowleaf trefoil, tall wheatgrass, and alkali sacaton were higher than those determined for earlier harvests, whereas $K^+:Na^+$ selectivity of

Table 1
Potassium–sodium and potassium–magnesium ratios in forages species grown in greenhouse sand cultures and in the saline–sodic solutions used to irrigate the crops

Forage	EC (dS m^{-1})	K/Na[a] (plant)	K/Na[b] (solution)	$S_{K,Na}$	K/Mg[a] (plant)	K/Mg[b] (solution)	$S_{K,Na}$
Alfalfa, Salado (3)[a]	15	2.7b[b]	0.023	113	7.3a	0.21	35
Alfalfa, Salado (3)	25	1.4b	0.016	89	3.3b	0.15	22
Alfalfa, SW9720 (3)	15	2.5a	0.023	104	7.3a	0.21	36
Alfalfa, SW9720 (3)	25	1.6b	0.016	96	3.6b	0.15	24
Narrowleaf trefoil (2)	15	1.6a	0.032	50	6.7a	0.28	24
Narrowleaf trefoil (2)	25	0.58b	0.021	26	4.0b	0.19	21
Broadleaf, trefoil (1)	15	0.37a	0.032	12	1.6a	0.28	6
Broadleaf, trefoil (1)	25	0.20b	0.021	8	0.97b	0.19	5
Tall wheatgrass (3)	15	0.98a	0.032	31	5.6a	0.28	20
Tall wheatgrass (3)	25	0.84b	0.019	44	5.6a	0.17	41
Alkali sacaton (2)	15	0.67a	0.032	21	3.7a	0.28	13
Alkali sacaton (2)	25	0.60a	0.019	31	3.6a	0.17	21
Kikuyugrass (3)	15	11.2a	0.027	402	4.6a	0.23	20
Kikuyugrass (3)	25	5.6a	0.017	303	4.0b	0.15	26
Paspalum PI299042 (2)	15	3.3a	0.034	99	5.3a	0.29	18
Paspalum PI299042 (2)	25	2.9a	0.023	126	5.3a	0.15	27
Paspalum Polo (2)	15	1.3a	0.034	38	4.8b	0.29	16
Paspalum Polo (2)	25	1.1b	0.023	47	5.5a	0.15	28
Bermudagrass (1)	15	6.6b	0.027	237	4.5b	0.23	28
Bermudagrass (1)	25	6.0a	0.017	341	5.1a	0.15	33

Selectivity coefficients ($S_{K,Na}$) and ($S_{K,Mg}$) were calculated by the method described by Flowers and Yeo (1988).

[a] Ion data from early harvest numbers as indicated.

[b] Within columns and species (or genotypes), means followed by a different letter are significantly different at the 0.05 probability level according to Tukey's studentized range test.

kikuyugrass, the paspalums, and bermudagrass decreased over time (data not shown).

Neither K$^+$/Na$^+$ ratios nor K$^+$:Na$^+$ selectivity coefficients appear to be satisfactory indicators of relative salt tolerance of the forages examined in this study. Alkali sacaton, tall wheatgrass, kikuyugrass, and bermudagrass are rated as salt-tolerant crops. The K$^+$/Na$^+$ ratios calculated for kikuyugrass and bermudagrass grown at 15 dS m^{-1} were 11.2 and 6.6, respectively. As salinity increased to 25 dS m^{-1}, both ratios dropped significantly, but were still well above the recommended value for adequate crop nutrition (Table 1). In contrast, K$^+$/Na$^+$ ratios for the equally salt-tolerant grasses, tall wheatgrass and alkali sacaton, were <1 at both levels of salinity. Selectivity coefficients also differed widely for these salt-tolerant grasses. For example, kikuyugrass and bermudagrass showed strong preference for K$^+$ over Na$^+$, with selectivity coefficients 8- to 10-fold higher than values for tall wheatgrass and alkali sacaton.

The adequate range for Mg^{2+} in glycophytes is unusually broad, mainly due to competing effects of K$^+$. Plants with high K$^+$ contents; therefore, also require high Mg^{2+} to insure adequate Mg^{2+} nutrition. For example, the Mg^{2+} requirement for alfalfa ranges from 123 to 329 mmol kg^{-1}; K$^+$ requirement ranges from 640 to 972 mmol kg^{-1} (Marschner, 1995). At moderate salinity, both alfalfa cultivars evaluated in our study were strong K$^+$

accumulators and showed a decided preference for K^+ over Mg^{2+}. Over the course of the experiment, Mg^{2+} in alfalfa grown in the 15 dS m^{-1} treatment (Figs. 1 and 2) was 106 mmol kg^{-1} dry wt., slightly below the lower end of the concentration range (0.3%, 123 mmol kg^{-1} dry wt.) recommended for adequate Mg^{2+} status. However, neither alfalfa cultivar showed visible symptoms of Mg^{2+} deficiency. Both the K^+/Mg^{2+} ratios and the selectivity of K^+ over Mg^{2+} in alfalfa and narrowleaf trefoil significantly decreased as salinity increased and external Mg^{2+} rose from 14 to 28 mM (Table 1). Potassium–magnesium relations in the grasses differed markedly from the legumes inasmuch as increases in external Mg^{2+} had very little influence on K^+/Mg^{2+} ratios. Selectivity coefficients for the grasses, in contrast to the legumes, increased as salinity increased from 15 to 25 dS m^{-1}. Averaged over the duration of the experiment, the selectivity for K^+ over Mg^{2+} decreased in all species (data not shown). This effect was primarily the result of significant decreases in shoot-K, as the plants aged.

As external Ca^{2+}/Mg^{2+} decreased from $\sim$0.8 at moderate salinity to $\sim$0.4 at 25 dS m^{-1}, Ca^{2+}/Mg^{2+} in the herbage also decreased, although for many of the grasses this effect was not significant (Table 2). Calcium is strongly competitive with Mg^{2+}, and binding sites on root membranes appear to have less affinity for the highly hydrated Mg^{2+} than for Ca^{2+} (Marschner, 1995). Selectivity for Ca^{2+} by all the forages increased with increasing

Table 2
Calcium–magnesium and chloride–sulfate ratios in forages species grown in greenhouse sand cultures and in the saline–sodic solutions used to irrigate the crops

Forage	EC (dS m^{-1})	Ca/Mg[a] (plant)	Ca/Mg[b] (solution)	$S_{Ca,Mg}$	Cl/SO$_4$[a] (plant)	Cl/SO$_4$[b] (solution)	$S_{Cl,SO4}$
Alfalfa, Salado (3)[a]	15	2.6a[b]	0.84	3.0	2.1a	0.99	2.1
Alfalfa, Salado (3)	25	1.8b	0.44	4.1	0.82b	1.1	0.82
Alfalfa, SW9720 (3)	15	2.5a	0.84	3.0	2.7a	0.99	2.7
Alfalfa, SW9720 (3)	25	1.8b	0.44	4.1	0.91b	0.1	0.91
Narrowleaf trefoil (2)	15	1.5a	0.85	1.8	4.2a	1.0	4.1
Narrowleaf trefoil (2)	25	1.1b	0.43	2.5	3.4b	0.96	3.6
Broadleaf, trefoil (1)	15	1.2a	0.81	1.4	3.0a	1.0	2.9
Broadleaf, trefoil (1)	25	0.67b	0.43	1.6	1.6b	0.96	1.7
Tall wheatgrass (3)	15	0.66a	0.81	0.82	9.1a	1.0	8.9
Tall wheatgrass (3)	25	0.46b	0.43	1.1	6.9b	1.1	6.3
Alkali sacaton (2)	15	0.70a	0.81	0.87	2.2a	1.0	2.1
Alkali sacaton (2)	25	0.68a	0.43	1.6	2.4a	1.1	2.1
Kikuygrass (3)	15	0.34a	0.81	0.42	8.0a	1.1	7.6
Kikuygrass (3)	25	0.29a	0.43	0.67	6.5b	1.1	5.9
Paspalum PI299042 (2)	15	0.60a	0.88	0.68	1.5a	1.0	1.5
Paspalum PI299042 (2)	25	0.60a	0.43	1.4	1.2b	1.1	1.1
Paspalum Polo (2)	15	0.55a	0.88	0.63	0.99a	1.0	0.94
Paspalum Polo (2)	25	0.59	0.43	1.4	0.56b	1.1	0.50
Bermudagrass (1)	15	0.97a	0.81	1.2	1.9b	1.1	1.9
Bermudagrass (1)	25	0.87a	0.43	2.1	2.7a	1.1	2.5

Selectivity coefficients ($S_{Ca,Mg}$) and ($S_{Cl,SO4}$) were calculated by the method described by Flowers and Yeo (1988).

[a] Ion data from early harvest numbers as indicated.

[b] Within columns and species (or genotypes), means followed by a different letter are significantly different at the 0.05 probability level according to Tukey's studentized range test.

salinity, despite the substantial increase in substrate Mg^{2+} relative to Ca^{2+}. The legumes were, in general, more selective for Ca^{2+} over Mg^{2+} than the grasses. The combined inhibitory effects of both Ca^{2+} and K^+ on Mg^{2+} uptake may have led to the relatively poor Mg^{2+} status of alfalfa grown at 15 dS m^{-1}. Averaged over the season, selectivity coefficients calculated for the legumes decreased compared to the values from a selected early harvest, whereas the grass species became more selective for Ca^{2+} over the growing season (data not shown).

Drainage effluents in the SJV contain high concentrations of SO_4^{2-} and Cl^-, typically in a molar ratio of ∼1:1 across salinity levels. The response of some of the forages to increasing anion concentrations in the irrigation waters was unexpected. Herbage S determined at all alfalfa harvests, for example, increased as salinity increased and the concentration of external S doubled. The two-fold increase in substrate Cl^-, however did not have a similar effect on shoot-Cl. In fact, shoot-Cl was significantly lower over the first four alfalfa harvests when plants were irrigated with water containing 111 mol m^{-3} Cl^- versus those containing 53 mol m^{-3}. Shoot-Cl in subsequent harvests was not affected by Cl^- concentration in the external solution. This response appears to be another example of SO_4^{2-} inhibition of Cl^- uptake (Fixen, 1993; White and Broadley, 2001).

Tall wheatgrass and kikuyugrass exhibited the highest Cl^-/SO_4^{2-} ratios and the strongest preference for Cl^- over SO_4^{2-} (Table 2). Selectivity coefficients tended, in general, to decrease as salinity increased. 'Polo' paspalum showed a slight preference for SO_4^{2-} over Cl^- in the 25 dS m^{-1} treatment.

Reports on effects of salinity on ion relations in plants are, in most cases, derived from single harvests. Relatively few studies are available which describe the time-course effect of ion accumulation under saline conditions. Our study illustrates species-specific differences in temporal effects on ion relations in salt-stressed forages, for example, the response of kikuyugrass to external Na^+ and SO_4^{2-} (Fig. 7). The accumulation of these ions in kikuyugrass shoots appeared to be closely regulated. Steady-state concentrations were achieved shortly after salinization and remained relatively unchanged for ∼300 days. Increases in shoot-Na and -SO$_4$ suggests that mechanism(s) operating to limit uptake of these ions became less effective with time under treatment, as shoot-Na increased two-fold over the next 30 days. Ion analysis based on a single harvest may not be sufficient to evaluate other important ion relationships that affect forage mineral quality for ruminant nutrition.

This year-long screening trial identified selected forages, which are good candidates for production in the saline drainage water reuse systems proposed for the San Joaquin Valley of California. Although plant growth was inhibited by salinity stress (Grattan and Oster, 2003), there are strong indications that, baring other stress factors, reuse systems which include these species would be sustainable. Complex ion ratios and balances in the saline irrigation waters did not adversely affect plant nutrient status and, with the exception of broadleaf trefoil, none of the forages showed symptoms of ion toxicities or deficiencies. Additional information on biomass production (Grattan et al., 2004a) and forage quality (Robinson et al., 2003) and (Grattan et al., 2004b) will aid in selecting the most successful candidates for further evaluation under field conditions.

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